THE QUEEN ANT AS A PSYCHOLOGICAL STUDY

By Dr. WILLIAM MORTON WHEELER

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OBSERVERS of ant behavior have almost invariably fixed their attention on the easily procurable workers, to the all but complete neglect of the males and queens. In the case of the males, this neglect is, perhaps, pardonable, for the behavior of this sex is extremely monotonous. The neglect of the queens, however, as I shall endeavor to show, has not only left untouched a very interesting subject of study, but is responsible for much useless speculation.

Mention of the queen ant unfortunately suggests by association the idea of the queen honey-bee. These two insects are, however, in certain very important respects diametrical opposites. The queen honey-bee is a degenerate creature, unable to nourish herself or her young, to visit the flowers, build or store the comb; while the worker bee, apart from her normal infertility, still retains intact all the true female attributes of the ancestral solitary bees. In ants the very reverse of this is true: the queen is the perfect exemplar and embodiment of the species and has lost none of the primitive female attributes of independence and initiative, which she shares with the female bumble bees, solitary and social wasps. The worker ant, on the contrary, bears all the stigmata of incomplete and retarded development. Although these differences between the queen honey-bee and queen ant and between the respective workers must be apparent to the most superficial observer, yet the familiar conception of the queen honey-bee as little more than an egg-laying machine, so degenerate that she can not exist apart from the workers, has been tacitly expanded to embrace the queen ant. Surely it is time that the reputation of this insect should be viewed in a more favorable light.

Let us follow as briefly as possible the eventful life history of the queen ant. After more protracted larval and pupal stages than those of the worker and male—more protracted in order that she may store up more food and hence more energy in her body—she hatches as a sensitive callow in a colony at the height of its annual development. In other words, she is born into a community teeming with queens, workers and males, and the larvæ and pupæ of these various forms at the season of their greatest activity and growth. From all sides a shower of stimuli must be constantly raining in upon her delicate organization as she tarries for days or even weeks in the dark galleries of the parental

Fig. 1. Incipient Colony of Carpenter Ant (*Camponotus pennsylvanicus*), consisting of the queen, three minim workers and a packet of young larvæ, inhabiting the abandoned pupa case of a beetle (*Rhagium lineatum*) under pine bark. About natural size.

nest, while her color gradually deepens and her integument acquires its mature consistency. During this her prenuptial life, she may assist the workers in carrying about, feeding and cleaning the brood. She eats independently of the food brought into the nest by the foraging workers. She may occasionally join the workers in excavating chambers and galleries. If she belongs to a slave-making species she may even accompany the workers on their cocoon-robbing expeditions. Although she shows that she is able to perform all these actions supposed to be peculiar to the workers, she often does so with a certain desultory incoherency.

When fully mature she becomes impatient for her marriage flight and must often be forcibly detained in the nest by the workers till the propitious hour arrives when the males and females from all the nests in the neighborhood rise high into the air and celebrate their nuptials.

Then the fertilized queen descends to the earth and at once divests herself of her wings, either by pulling them off with her legs and jaws or by rubbing them off against the grass-blades, pebbles or soil. This act of deälation is the signal for important physiological and psychological changes. She is now an isolated being, henceforth restricted to a purely terrestrial existence, and has gone back to the ancestral level of the solitary female Hymenopteron. During her life in the parental nest she stored her body with food in the form of masses of fat and bulky wing-muscles. With this physiological endowment and with an elaborate inherited disposition, ordinarily called instinct, she sets out alone to create a colony out of her own substance. She begins by excavating a small burrow, either in the open soil, under some stone or in rotten wood. She enlarges the blind end of the burrow to form a small chamber and then completely closes the opening to the outside world.

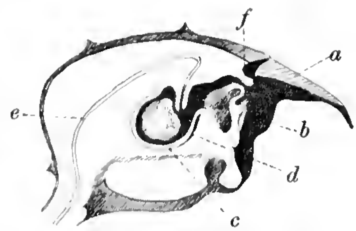

FIG. 2. HEAD OF A RECENTLY FERTILIZED QUEEN OF *Atta sexdens* LONGITUDINALLY BISECTED; *a*, mandible; *b*, labium retracted; *c*, buccal pocket, containing *d*, the pellet of fungus hyphæ carried from the parental nest, *e*, œsophagus, *f*, oral orifice. (After J. Huber.)

The labor of excavating often wears away all her mandibular teeth, rubs the hairs from her body and mars her burnished or sculptured armor, thus producing a number of mutilations, which, though occurring generation after generation in species that nest in hard, stony soil, are, of course, never inherited. In the cloistered seclusion of her chamber the queen now passes days, weeks, or even months, waiting for the eggs to mature in her ovaries. When these eggs have reached their full volume at the expense of her fat-body and degenerating wing-muscles, they are fertilized with a few of the many thousand spermatozoa stored up in her spermatheca and laid. The queen nurses them in a little packet till they hatch as minute larvæ. These she feeds with salivary secretion derived by metabolism from the same source as the eggs, namely, from her fat-body and wing-muscles. The larvæ grow slowly, pupate prematurely and hatch as unusually small but otherwise normal workers. In some species it takes fully ten months to bring such a brood of minim workers to maturity, and during all this time the queen takes no nourishment, but merely draws on her reserve tissues. As soon as the workers mature, they break through the soil and thereby make an entrance to the nest and establish a communication with the outside world. They enlarge the original chamber and continue the excavation in the form of galleries. They go forth in search of food and share it with their exhausted mother, who now exhibits a further and final change in her behavior. She becomes so exceedingly timid

FIG. 3 EGGS AND FUNGUS GARDEN IN CELL OF QUEEN *Atta sexdens* FORTY-EIGHT HOURS AFTER THE NUPTIAL FLIGHT. (After J. Huber.)

FIG. 4. EGGS AND FUNGUS GARDEN IN CELL OF QUEEN *Atta sexdens* SEVENTY-TWO HOURS AFTER THE NUPTIAL FLIGHT. (After J. Huber.)

and sensitive to the light that she hastens to conceal herself on the slightest disturbance to the nest. She becomes utterly indifferent to the young, leaving them entirely to the care of the workers, while she limits her activities to laying eggs and imbibing liquid food from the tongues of her attendants. This copious nourishment soon restores her depleted fat-body, but her disappearing wing-muscles have left her thoracic cavity hollow and filled with gases which cause her to float when placed in water. With this circumscribed activity she lives on, sometimes to an age of fifteen years, as a mere egg-laying machine. The current reputation of the ant queen is derived from such old, abraded, toothless, timorous queens found in well-established colonies. But it is neither chivalrous nor scientific to dwell exclusively on the limitations of these decrepit beldames without calling to mind the charms and self-sacrifices of their younger days.

FIG. 5. SILHOUETTE OF A QUEEN *Atta sexdens* IN THE ACT OF MANURING HER FUNGUS GARDEN. A tuft of fungus mycelium is torn out of the garden, placed against the anus and saturated with a drop of fecal liquid. (From an instantaneous photograph, after J. Huber.)

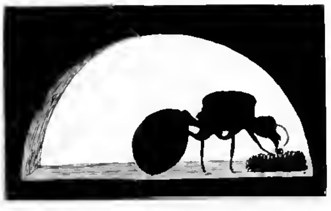

FIG. 6. SILHOUETTE OF A QUEEN *Atta sexdens* REPLACING THE SATURATED TUFT OF MYCELIUM IN THE FUNGUS GARDEN. (From an instantaneous photograph, after J. Huber.)

Now to bring up a family of even very small children without eating anything and entirely on substances abstracted from one's own tissues is no trivial undertaking. Of the many thousands of ant queens annually impelled to enter on this ultra-strenuous life, very few survive to become mothers of colonies. The vast majority, after starting their shallow burrows, perish through excessive drought, moisture or cold, the attacks of parasitic fungi or subterranean insects, or start out with an inade-

quate supply of food-tissue in the first place. Only the very best endowed individuals live to preserve the species from extinction. I know of no better example of natural selection through the survival of the fittest.

It is certain that the colonies of most species are founded in the manner here described. It is certain, moreover, that all this is rendered possible by the nutritive endowment of the queen. As the winged germ of the species she has all the advantages that a yolk-laden has over a comparatively yolkless egg. Now among the 5,000 known species of ants we should expect to find considerable differences in the quantity of nutriment stored up in the young queen. And this is unquestionably the case. In some species the queens are of enormous size, in others they are very small compared with the workers. And since queens of

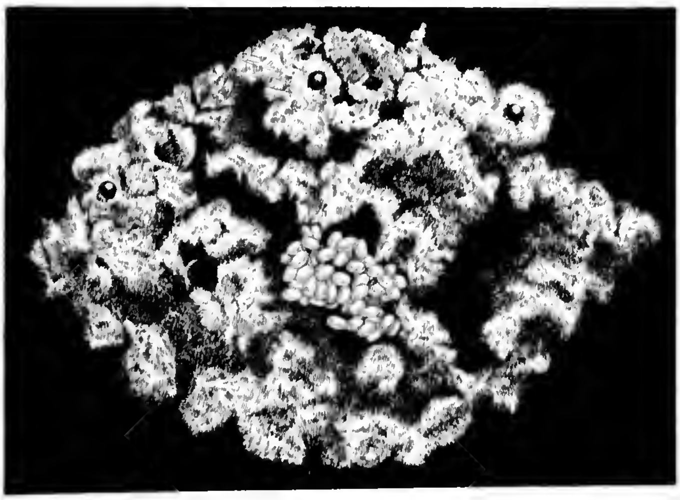

FIG. 7. FUNGUS GARDEN OF *Atta sexdens* FOURTEEN DAYS AFTER THE NUPTIAL FLIGHT. There are about 100 eggs which the queen has placed in a depression in the middle of the garden. Near the periphery there are three drops of the fecal liquid with which the queen manures the garden (After J. Huber.)

average dimensions are able to start colonies by themselves alone, we should expect that unusually large queens would be able to accomplish even more, and very small queens less. This, too, is borne out by observation.

Unusually large queens are found in the genus *Atta*, a group of American ants that raise fungi for food, and are, so far as known, quite unable to subsist on anything else. The female *Atta* on leaving the parental nest, is so well endowed with food-tissue, that she not only can raise a brood of workers without taking nourishment, but has energy to spare for the cultivation of a kitchen garden. She carries the germ of this garden from the parental nest in the form of a pellet of fungus

hyphæ stowed away in her buccal pocket, spits it out soon after completing her chamber, manures with her excreta the rapidly growing hyphæ and carefully weeds them till her firstling brood of workers hatches. These then bring into the nest the pieces of leaves and the vegetable detritus essential to the maintenance and growth of the garden. The extraordinary habits of one of these fungus-raising ants, *Atta sexdens*, have been recently studied in great detail by Jakob Huber, from whose valuable paper I borrow a number of the accompanying illustrations (Figs. 2 to 7).

Very different is the condition of certain queen ants poorly endowed with food-tissue—especially of some whose bodies are actually smaller than the largest workers of their species. Such queens are quite unable to bring up colonies unaided. They are therefore compelled, after fertilization, to associate themselves with adult workers either of their own or of a closely allied species. In the former case the queens may either remain in the parental nest and omit the nuptial flight, or return to the parental or to some other colony of the same species. In either case they add to the reproductive energy of an already established colony and thus prolong its life. If one of these poorly endowed queens, however, happens to alight from her nuptial journey far from any colony of her own species, she is obliged to associate with alien workers. And in this case, according to the species to which she belongs, one of three courses is open to her.

First, she may secure adoption in a small queenless colony of an allied species. Here she is fed, lays her eggs and the resulting larvæ are reared by the strange workers. Eventually the alien workers die off and leave the queen and her own workers as an independent and sufficiently established colony, capable of rapid and often enormous multiplication. This is temporary social parasitism, first observed by myself in some of our American ants, but since found in some of the European species where I predicted its occurrence.

Second, the poorly endowed queen may establish herself in a colony of another species, but be unable, even after her workers have matured, to survive the death of the host colony, except, perhaps, by migrating to another nest of the same species. This is permanent social parasitism.

Third, the queen may enter a small colony of alien workers, and, when attacked, massacre them, appropriate their larvæ and pupæ, carefully secrete and nurse them till they hatch and thus surround herself with a colony of young and loyal workers that can bring up her brood for her without any drain on her food-tissues. This is the method of colony formation adopted by queens of the slave-making ants, as I have found by a number of experiments during the past summer. These queens thus manifest an instinct, hitherto supposed to be exclusively peculiar to the workers, namely the instinct to rob the larvæ and pupæ of another species and bring them up as auxiliaries, or slaves.

Although the foregoing facts belong to ethology rather than to comparative psychology, it seemed necessary to review them before emphasizing their bearing on certain general questions. The behavior of the queen ant may be said to depend, first, on a relatively fixed inherited predisposition, or instinct; second, on inherited plasticity or adaptability; third, on constantly changing physiological states, and fourth, on stimuli which are partly primary and external and partly secondary, internal or true stimuli. These last are probably identical, as suggested by Jennings and others, with the physiological states, which in turn are evidently to be conceived as metabolic processes. That the queen ant profits by her prenuptial sojourn in the parental nest to learn by experience, tradition and imitation, I have no doubt, but queens hatched in isolation show that this acquisition is insignificant in comparison with the inherited instincts. These appear as elaborate catenary reflexes, of which the reactions to light and contact stimuli may be taken as examples. In her callow stages the queen is negatively phototropic and positively stereotropic, but as the time for her nuptial flight approaches, these reactions are reversed, so that she seeks the light and avoids contact with the walls of the nest. After fertilization she again returns to the prenuptial condition—she shuns the light and tries to bury herself in the soil or under stones. These reactions, first described by Loeb, are as irresistible as they are adaptive. It can be shown, moreover, that these changes in tropisms are accompanied by changes in other instincts. My attention was first directed to the stereotyped character of these reactions in the queen ant by a simple experiment. I found that merely pulling off the wings with the tweezers caused the insect to pass at once from positive phototropism and negative stereotropism to the reverse. This shows that the change is not caused by fecundation, since artificially deälated virgin queens went through the complex catenary reflex of founding a colony with the same precision as fertilized individuals.

These and other observations, which I am unable to give in the space at my disposal, all point to constantly changing metabolic states as the mainspring of the queen ant's behavior. She is, in fact, a veritable chemical laboratory, in which we can see more clearly than in many other animals, a direct relation between behavior and the flux of metabolism.

I hasten over this matter to another general problem. The discovery that the queen ant really possesses, at least *in potentiâ,* all the instincts of the worker, besides others peculiar to herself, puts a different construction on a matter which has long been puzzling theoretical zoologists. It has been taken for granted that worker ants are necessarily sterile and that they possess morphological, physiological and psychological characters not represented in the queens of their

species. On such assumptions it is, of course, impossible to understand how the workers can have come by the obviously adaptive and exquisitely correlated characters, which they are unable to transmit. It will be remembered that neo-Darwinians and neo-Lamarckians, in the persons of Weismann and Herbert Spencer, locked horns over this matter some years ago. Both in this and in many similar discussions, the very premises which both parties accepted are unwarranted. In the first place, it is now known that workers readily become fertile when well fed and that they can and often do produce normal young from unfecundated eggs. Although these young are usually, if not always, males, it is evident that these males, through the eggs which they fertilize, can transmit the characters of their worker mothers to succeeding generations of queens and workers. Thus the congenital, and perhaps even the acquired, characters of the worker are not necessarily lost, but can be gathered up into the germ-plasma of the species. In the second place, most, if not all of the characters of the worker are not qualitatively but only quantitatively different from those of the queen. In other words, the worker does not differ from the queen as a mutant, but as a fluctuating variation, which has been produced by imperfect or irregular feeding during its larval stages. This is true alike of morphological, physiological and psychological characters. Even when the queen fails to manifest the worker instincts, we are not justified in doubting her ability to do so under the proper conditions.

The hitherto unsuspected capacity of the queen ant is beautifully illustrated by another set of facts, which at the same time show the close connection between adaptive behavior and regulation, or regeneration. Under normal conditions the queen, after rearing a brood of workers, no longer takes part in the 'muck and muddle of child-raising' but seems to be as indifferent to the young of her species as some women who have brought up large families. If, however, the firstling brood of workers be removed and the queen isolated, she forthwith begins to bring up another brood, precisely as in the first instance, provided her body still contains sufficient food-tissue. She thus regenerates the lost part of her colony, just as a mutilated earthworm regenerates its lost segments. In the ant the absence of workers acts as a stimulus to restore the colony, just as the absence of segments leads the earthworm to complete its body.

The regulatory activities of the queen ant are, of course, highly adaptive and hence evidence of the variability which is so clearly manifested in the physical structure of these insects. There is no contradiction in the coexistence of such variability with the very stable character of certain instincts like those to which I have called attention, for an organism may be extremely plastic in some of its activities and rigidly conservative in others. It is evident that the remarkable vari-

ability of the female sex in ants—including under this term both the fertile, or queen phase, and the usually sterile, or worker phase—reaches its clearest expression in the extraordinary range of intraspecific polymorphism. In certain species, for example in the African driver ants (*Dorylii*) and American ants of visitation (*Ecitonii*), the structural differences between the workers of the smallest caste and the huge queen of the same species are enormous and represent an amplitude of variability in the female sex unequalled in any other organisms. Male ants, on the contrary, exhibit so little variability that it is often difficult, or even impossible, to distinguish the genera of single specimens of this sex. These facts have an important bearing on the views of authors like Brooks and Geddes and Thomson who assume that male animals are more variable than females, and of those authors who have transplanted this hypothesis to the fields of sociology and anthropology. All of these writers maintain a discreet and significant silence on the subject of the social insects. Equally astonishing, however, is the attitude of the biometricians, who, priding themselves on the accuracy of their methods and repudiating mere observation and speculation, proceed to an elaborate measurement of the wings of honey-bees and ants for the purpose of ascertaining whether males are more variable than females, when a glance at the personnel of a few ant and termite colonies would convince the most skeptical that there can be no such correlation between sex and variability as that assumed by the above-mentioned authors. If it is clear that the males of many of the higher animals are in certain characters more variable than the cospecific females, it is even clearer that the very opposite is true of the social hymenoptera, while in the termites, or white ants, both sexes seem to be alike variable and polymorphic.